The second most abundant shrub on the core and peripheral plots was *Chrysothamnus viscidiflorus* (Figs. 4, 5, Table 1). Although *A. tridentata* cover decreased markedly after 1975, *C. viscidiflorus* cover generally increased over the 45 years, especially on the core plots (Fig. 5) where cover of *C. viscidiflorus* in 1995 was 6.3 times that in 1950.

The substantial increase in shrub cover between 1957 and 1965 (Fig. 4) corresponded with the high precipitation received during that period (Fig. 5). Because density of the most common shrubs did not increase during that period (Fig. 8), the increase in cover apparently resulted largely from increases in the size of existing shrubs rather than from recruitment of new individuals.

Perennial grasses contributed much less cover than shrubs on both core and peripheral plots (Table 1, Fig. 4). On the core plots, cover of perennial grasses increased exponentially from 0.46% in 1950 to 6.2% in 1975. Following this 13-fold increase, perennial grass cover decreased and has fluctuated between 1.4 and 4.0% in recent samples. The peak in perennial grass cover apparently lagged behind that of shrubs by a decade, but this may reflect the lack of data for intervening years.

Cover of each of the most common grasses on the core plots increased many fold between 1950 and 1975 (Fig. 5). Cover of *Elymus elymoides*, *Oryzopsis hymenoides*, and *Stipa comata* declined sharply after 1975, while that of the agropyrons and *Poa* (data not shown) remained high between 1975 and 1983, but then dropped precipitously by 1985. Cover of the agropyrons, *E. elymoides*, and *S. comata* increased between 1985 and 1990, and all but the agropyrons remained high in 1995 (Fig. 5). In contrast, cover of *O. hymenoides* has remained low over the past decade, at about the same level that it was in 1957.

In most cases, cover of shrubs and perennial grasses was not correlated with precipitation received in the years the samples were taken, and in no case was cover of a member of either group correlated with precipitation received in the year preceding the sample year (Table 3). However, a number of significant relationships between cover and precipitation received from 3 to 5 years earlier were found (Table 3, Fig. 6). The only significant correlations between cover and precipitation in the sample year were for *Atriplex confertifolia* and the poas (Table 3). Cover of *A. confertifolia* was also correlated with average precipitation received over the previous 3, 4, and 5 years (Table 3). On the core plots, cover of the agropyrons and of *Stipa comata* were

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positively correlated with total annual precipitation received 5 years earlier, resulting in a marginally significant correlation between total perennial grass cover and total annual precipitation with a similar lag time (Fig. 6). Total shrub cover was positively correlated with total annual precipitation received 3 years earlier and similar trends were apparent for *Artemisia tridentata* (4-year lag) and *Chrysothamnus viscidiflorus* (5-year lag with growing season precipitation, Fig. 6). Surprisingly, for the core plots there was a strong negative correlation between cover of *Tetradymia canescens* and growing season precipitation received 4 years earlier (Fig. 6), with a similar trend on the peripheral plots (Table 3).

*Long-term trends in density of plants.* There were no obvious correlations between long-term changes in plant density and precipitation patterns (Figs. 7, 8). Trends on core and peripheral plots were similar, so data for the core plots only are shown. Mean density of shrubs on the core plots has changed little over 45 years, but the standard errors for mean shrub densities for 1950 and 1957 were much higher than those for subsequent years (Fig. 7). Density of the dominant shrub, *Artemisia tridentata*, decreased considerably in recent decades as a consequence of widespread die-off (Fig. 8). In this case, there was a corresponding decrease in cover of *A. tridentata* (Fig. 5). Concomitantly, both cover (Fig. 5) and density (Fig. 8) of the next most common shrub, *Chrysothamnus viscidiflorus*, increased. There was no consistent trend in the density of the only common succulent on the study area, *Opuntia polyacantha* (Fig. 8).

Mean density of perennial grasses appears to have changed little between 1950 and 1978 but then increased sharply and was over two-fold higher in 1985 than in previous sample years (Fig. 7). Although the density of the most common grasses increased over the last 2 decades, the years of highest density did not coincide. Density of the agropyrons and *Elymus elymoides* peaked in 1985 during a wet period, while that of *Stipa comata* was highest in 1990, during a drought (Fig. 8). Density of those three groups fluctuated widely in the most recent samples, whereas that of *Oryzopsis hymenoides* has fluctuated little over the entire 45 years (Fig. 8).

The mean density of perennial forbs remained quite low between 1950 and 1965, but increased significantly over the past 2 decades (Fig. 7); forb density in 1995 was about three times that recorded in the earliest samples. Density of annuals has varied considerably, but no trend is apparent (Fig. 7). Density of annuals was much higher in 1975 than in any other sample

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year, apparently a consequence of abundant precipitation and a cool spring and early summer (R. Jeppson, personal communication).

In most cases, trends for density have not paralleled those for cover. For perennial grasses, shrubs, and for all but one of the common species in those groups, mean cover was not correlated with mean density across the 8 years for which both cover and density were sampled. This was true for the core plots and for the core plus peripheral plots. The only species for which this relationship was significant was *Stipa comata* (core plots, $r = 0.73$, $n = 8$, $P = 0.042$; all plots, $r = 0.70$, $n = 8$, $P = 0.056$).

*Trends in species richness and relationships between richness and cover*. The mean species richness of shrubs, perennial grasses, and perennial forbs recorded on the line-intercept transects and in the density quadrats of the core plots generally increased from 1950 to 1995 (Fig. 9). The rate of increase in richness was higher for perennial grasses than for shrubs. The mean number of perennial grass species recorded on the line-intercept transects and of forbs in the density quadrats also increased significantly with time on the peripheral plots, but that of shrubs did not (Fig. 9). The mean number of species of annuals was more variable, with richness being highest in 1975 and 1995, census years that had high spring/early summer precipitation (Figs. 3, 9).

In 1950, perennial grasses were recorded on the line interception transects at 23 of the 35 core plots that were sampled in each of the 9 census years (Fig. 10). That number increased with each successive sampling through 1975; since then perennial grasses have been recorded by line interception at all 35 plots. Similar trends are seen in pooled cover and density data (Table 4). Although the number of plots upon which individual species of perennial grasses has generally increased over the 45 years of record, there is considerable variability through time as a species appears and then disappears on individual plots (Fig. 10, Table 4). For example, *Oryzopsis hymenoides* was recorded in cover data at 10 plots in 1965, at 26 in 1975, but only at 16 in 1978. Similarly, *Stipa comata* was recorded in either cover or density data at 17 plots in 1957, at 12 in 1965, and at 22 in 1975 (Table 4). The number of plots where *Chrysothamnus viscidiflorus* was recorded has fluctuated much less but has increased sharply since 1978 (Fig. 10, Table 4).

Despite the increases in mean species richness per plot, the aggregate species richness for shrubs and perennial grasses on the core plots has changed little (Table 4). Only three species of perennial grasses, *Sporobolus cryptandrus*, *Stipa thurberiana*, and *Elymus triticoides* occurred in

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recent censuses but not in early ones. It is unlikely that any of these are new immigrants to the general area sampled by the core plots.

Cover of shrubs and of perennial grasses typically was higher on plots having higher species richness. Cover of both shrubs and perennial grasses was positively correlated with species richness in 6 of 9 census years (Figs. 11, 12), but the years in which those relationships were significant did not always coincide. Consistent with these results for individual years, average cover of shrubs was positively correlated with average shrub species richness, and average perennial grass cover was positively correlated with average perennial grass species richness (Fig. 13).

Cover of shrubs and perennial grasses combined was significantly correlated with combined species richness in 4 of 9 years, and in each case the relationship was positive. Likewise, average cover of shrubs and perennial grasses combined, on 35 plots over 9 census years, was positively correlated with average species richness of shrubs and perennial grasses ($r = 0.40$, $P = 0.016$).

For the subset of 35 plots sampled in 9 years, average change in shrub cover was positively correlated with average shrub species richness, indicating that absolute shrub cover changed more on plots having more species of shrubs (Fig. 13). Average change in perennial grass cover was not significantly correlated with average perennial grass species richness, however, there was a tendency for change in grass cover to be higher on plots having higher species richness (Fig. 13). For the core and peripheral plots combined, which were sampled in fewer years, the relationship between average change in cover and average species richness was significant and positive for both shrubs and perennial grasses. Change in cover of shrubs and perennial grasses combined was positively correlated with combined average species richness for the 35-plot subset ($r = 0.35$, $P = 0.037$) and for the core plus peripheral plots ($r = 0.24$, $P = 0.034$).

The standard deviation in shrub cover was positively correlated with the average number of shrub species recorded on a plot (Fig. 13). This relationship was not significant for perennial grasses, but there was a tendency for the standard deviation to be larger on plots having more species (Fig. 13). The coefficient of variation (CV) of cover was negatively correlated with average species richness of both shrubs and perennial grasses (Fig. 13). Thus, for each of these plant groups, there was relatively less variation in cover where species richness was higher.

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For the subset of 35 plots, standard deviation of cover of shrubs and perennial grasses combined was positively correlated with average combined species richness ($r = 0.37$, $P = 0.03$). For the same plots, CV of cover of shrubs and perennial grasses combined was not significantly correlated with average combined species richness ($r = 0.040$, $P = 0.25$).

We found no significant correlation between species richness and the magnitude of the change in percent similarity as measured by the minimum, the maximum, or the mean of the plotwise year-to-year comparisons ($P > 0.1$ in all cases). Thus stability in species composition did not appear to be related to species richness

*Relationships between shrub and grass cover, and changes in plot similarity through time.* Figure 14 shows perennial grass cover plotted against shrub cover for the core plots. There were significant negative correlations between cover of perennial grasses and shrubs in 7 of the 9 sample years; the negative correlation was marginally significant in 1985 as well

This analysis also shows that the plots have become much more heterogeneous in terms of vegetal cover since 1950. In 1950, shrub cover ranged from 1.2% to 30%, whereas values ranged from 3% to 48% in 1975 and from 1.2% to 62% in 1995. This increase in heterogeneity is apparent in the amount of scatter on the abscissa of Figure 14. In 1950, cover of perennial grasses ranged from 0 to 6.5%, whereas values ranged from 0.6% to 27% in 1975 and 0.6% to 8% in 1995. Scatter on the ordinate of Fig. 14 reflects the fluctuations in grass cover.

· This increase in heterogeneity is also reflected in a large decrease in percent similarity among the core plots over the 45 years of record (Fig. 15). Mean percent similarity at each census decreased linearly with time, from 72% in 1950 to 40% in 1995.

## Discussion

*Long-term trends in species abundances, species richness, and similarity among plots.* Numerous studies of semiarid ecosystems indicate that once woody species become dominant as a result of overgrazing or alteration of natural disturbance regimes (e.g., fire suppression) the resulting cohort of unpalatable woody plants may persist for long periods (e.g. Smiens et al. 1976, Rice and Westoby 1978, Austin and Williams 1988, Westoby et al. 1989, Milton et al. 1994, Wiegand and Milton 1996) Dominance by woody species often is accompanied by loss of biodiversity and low productivity of palatable herbaceous plants. The inertia in such communities is a consequence of

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the longevity of individuals of woody species, the usurping of resources by mature individuals of those species, and the relative paucity of propagules of herbaceous species. Contemporary models of vegetation dynamics in such systems postulate that the vegetation can exist in one of various relatively stable states and that transitions between states may require some biotic or abiotic force to drive the system over some threshold (Westoby et al. 1989, Tausch et al. 1993). Thus, we might predict that, in the absence of a major disturbance, the vegetation of a shrub-steppe heavily dominated by a relatively long-lived woody species would be quite static.

The 1950 data are consistent with the suggestion (Harniss and West 1973a) that the area was heavily grazed by domestic livestock prior to the establishment of the INEEL. Very low cover of perennial grasses, low density and richness of perennial forbs, dominance of plots by shrubs, primarily *A. tridentata*, and relative homogeneity of plots with respect to perennial grass and shrub cover are all consistent with differential responses of species to heavy grazing. However, the composition and structure of the vegetation in 1950 also may have been influenced by the prolonged drought conditions through the 1930's and 1940's (Fig. 3). Under drought conditions, stress-tolerant shrubs such as *A. tridentata* may persist while faster-growing and relatively short-lived species such as perennial grasses and forbs may suffer considerable mortality. In this context, it is important to note that there was little change in the vegetation between 1950 and 1957, a period during which precipitation was below average.

Despite these initial conditions, the vegetation on the permanent plots at the INEEL has been anything but static over the past 45 years. After the first 2.5 decades, perennial grass cover on the core plots was 13 times that recorded initially. Subsequently it has fluctuated over 4-fold, from 6.2% in 1975 to 1.4% in 1985, but it has remained high relative to 1950 (Fig. 4). Similar trends were apparent on the peripheral plots (Fig. 4). The substantial increase in cover of perennial grasses through 1975 did not come at the expense of the shrub overstory. Shrub cover increased markedly in the first 15 years and remained high through 1975 on the core plots and through 1985 on the peripheral plots; it has decreased recently as a result of widespread mortality of *Artemisia tridentata* (Fig 4). On the core plots, mean richness per plot of both shrubs and perennial grasses has increased (Fig. 9); nevertheless, data for perennial grasses indicate substantial rates of turnover of individuals within that functional group (Fig 10).

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What are the patterns and key drivers of these changes? Do the changes observed since 1950 merely represent stochastic fluctuations (sensu Miles 1979) driven by variability in precipitation, or can we identify directional changes indicative of successional development? There is no doubt that variability in precipitation has contributed to the documented changes in species composition and abundance. Shrub cover increased by over 50% in response to relatively high precipitation between 1957 and 1965, and it is likely that the exponential increase in cover of perennial grasses over the first 25 years reflected favorable moisture conditions in the 1960's and 70's (Fig. 3). The sampling frequency is not sufficient to determine how closely changes in cover may track precipitation, but correlation analyses indicate there may be 3- to 5-year lags in the responses of species or functional groups to precipitation patterns (Fig. 6).

Some of the cover data are difficult to reconcile with precipitation patterns, but differences in longevity and patterns of growth between shrubs and perennial grasses, coupled with lags between recruitment and mature size, are likely involved. Since the 1983 census, trends in cover of shrubs and of perennial grasses have been largely out of phase (Fig. 4). Following a generally wet period in the early 1980's, cover of both *Artemisia tridentata* and *Chrysothamnus viscidiflorus* had increased by 1985. Cover of perennial grasses in 1985, however, was anomalously low (Fig. 4), whereas their density was much higher than that recorded in any other year (Fig. 7). These data indicate substantial recruitment of perennial grasses in the early 1980's, but these recruits were apparently still very small in 1985. Density data (Fig. 7) suggest some mortality of perennial grasses during the drought of the late 1980's, but the survivors had increased sufficiently in stature to result in a 2.8-fold increase in perennial grass cover on the core plots from that in 1985 by 1990 (Fig. 4).

Species richness for the aggregate 35-plot sample has not changed appreciably since 1950 (Table 4); however, the data show a general, consistent increase in species richness per plot (Fig. 9). These results suggest that the increase in richness of individual plots was not a consequence of immigration of new species or species that had become locally extinct at the INEEL, but rather a consequence of expansions of species distributions within the study area. Populations that were small and isolated in 1950 have likely increased in size and distribution, thereby increasing the number of species found on a given plot. Anderson (1986) documented an increase in the distribution of perennial grasses on 35 plots and attributed that trend to greater availability of propagules as previously depleted grass populations increased between 1965 and 1975.

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Other than the increase in cover of perennial grasses during the first 2.5 decades and the general increase in average species richness, we found little evidence of directional changes in plant species composition. The only obvious directional change among the common shrub or perennial grass species was a consistent increase in the cover of *C. viscidiflorus*. There was no evidence of seral replacement among the perennial grasses, nor did members of this functional group tend to respond in concert through time (Figs. 5, 8, 10). Ordinations of the data from the core plots as well as from smaller subsets of plots having high similarity, using detrended correspondence analysis and non-metric multidimensional scaling (McCune and Mefford 1995), failed to identify any common trajectories of plots through time (results not shown). Species abundance data, then, do not suggest directional succession.

The 45-year period has witnessed a substantial increase in heterogeneity in vegetative structure among plots. Average percent similarity of the core plots decreased from 72% in 1950 to 40% in 1995 (Fig. 15). Thus, as the number of species per plot increased, the plots diverged in terms of their species composition and vegetative structure. This is not the result one might have predicted based on the traditional concept of range succession that envisions convergence on some climax composition (e.g. Huschle and Hironaka 1980), but we think that it is precisely the outcome that one might expect as a sagebrush rangeland recovers from a state that resulted from the combined effects of prolonged drought and livestock grazing.

Either extended drought or extensive grazing could have decreased the heterogeneity among plots as species less tolerant of drought or grazing were excluded from certain plots, leaving a larger proportion of plots dominated by drought or grazing-tolerant species. We believe this was the state of the study area when the plots were established in 1950. Increased precipitation coupled with reduced livestock grazing allowed species to respond to the small-scale differences in soil nutrients, infiltration, or runoff (on scales of 0.1 to 100 m) that create a mosaic of patches in which different species are superior competitors (sensu Tilman 1982).

Although the core plots cover an area that is fairly uniform with respect to soils, topography, and slope, these factors do vary among plots. Furthermore, samples taken at each plot cover an area large enough to include considerable variation in microtopography, soil depth, and soil resources. Substantial spatial variability in the concentrations of essential plant nutrients exists at the scale of individual plants in sagebrush steppe (Charley and West 1975, Jackson and

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Caldwell 1993 a, b, Ryel et al. 1996) Ryel et al. (1996) found that "patches of high internal uniformity" of soil nutrients were generally smaller than 2 m in diameter in a sagebrush community in southeastern Idaho.

In addition to deterministic competitive outcomes, it is likely that stochastic factors also contributed significantly to the observed increase in heterogeneity. Plant establishment depends on availability of propagules and arrival of those propagules at "safe sites" for germination (*sensu* Harper 1977). As depleted populations recover, arrival of propagules at suitable sites depends on a multitude of factors including proximity of source plants, dispersal characteristics of the propagules, barriers to dispersal (e.g., other plants, microtopography), and the vagaries of weather (wind speed and direction, rainfall amount and intensity). Priority effects may also be important as propagules arriving first may gain a competitive advantage over those arriving later.

Thus, we believe that the increases in plant species diversity and heterogeneity from 1950 to 1975 are largely the result of a recovery of vegetation from drought and grazing, reflecting an increase in the extent to which local variation in resource availability and stochastic variables determined the distribution and abundance of species. The increase in average species richness per plot (Fig. 9), the increase in average frequency of perennial grasses (Fig. 10, Table 4), and the increase in among-plot heterogeneity with time all are consistent with this conclusion. Even in the absence of major perturbations such as extended drought or overgrazing we can anticipate significant fluctuations in local plant species composition and abundance. Substantial fluctuations in cover of shrubs and perennial grasses from 1975 to 1995 (Fig. 4) may more accurately reflect the "normal" range of variation characteristic of sagebrush steppe. Variation in shrub and perennial grass cover on the core plots, measured by the standard deviation in cover, was substantially greater in 1975 than in earlier years, however it did not show a consistent increase after 1975.

These observations raise the question, at what scale should we expect models of successional or vegetation dynamics to apply? Daubenmire (1952) defined a "habitat type" as the collective area of land capable of supporting a specific plant association at climax. Daubenmire (1959) argued that a sample consisting of coverage estimates from fifty 0.2- x 0.5-m frames was sufficient to characterize an area. It seems quite clear that Daubenmire assumed that successional relationships would be manifest at the scale of the INEEL permanent plots. Most investigators

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who have inferred successional patterns from simultaneous samples of areas representing different seral stages or times since disturbance have made the same assumption. Examples in sagebrush steppe include Humphrey (1984) and Huschle and Hironaka (1980), who inferred successional patterns from the results of ordinations used to arrange individual areas. For such an assumption to hold, each plot would have to be representative of the range of variation found within the area potentially occupied by a particular association. Further, each plot would have to remain undisturbed at the scale of the sample plot for sufficient time for deterministic (e.g. competitive) interactions to be consummated. We think it is unlikely that either of these conditions generally holds in sagebrush steppe, and our data showing an increase in heterogeneity of the relative abundances of dominant species among plots supports that conclusion.

These observations make it clear that to understand the vegetation dynamics of even this relatively homogeneous sagebrush steppe a fairly large-scale perspective is needed. It is simply not possible to infer trends accurately from one or a few plots. The problems of scale in relation to "general laws" of succession were recently addressed by Brand and Parker (1995) in expanding on a successional model developed by Stewart Pickett and colleagues (Pickett et al. 1987, Pickett and McDonnell 1989). Their general framework for vegetation dynamics provides an insightful alternative to conventional models of succession. At the scale of an individual plot, vegetation development is dependent on and constrained by site availability for colonization and establishment, differential availability of propagules, and differential performance of the species available (Pickett et al 1987, Pickett and McDonnell 1989). All of these factors will vary from plot to plot, both spatially and temporally. For example, in the shrub steppe at the INEEL, small mammals may disturb the soil on some plots while harvester ants may create clearings on others. Mature sagebrush plants may die and provide openings for colonization on some plots but not others; such openings may be colonized by the exotic annual, *Bromus tectorum*, if it has been previously dispersed to that plot, or by any other species for which propagules are present. As a case in point, Plot 86 was dominated by sagebrush in 1985, with only a few *B. tectorum* plants recorded. By 1990, the sagebrush had died and *B. tectorum* was the dominant species present. In contrast, at other plots where sagebrush cover has been dramatically reduced, *B. tectorum* is either absent or a minor component of the vegetation.

The extent and timing of such small scale disturbances will vary from plot to plot and, when coupled with the vagaries of weather and propagule dispersal, will contribute to the

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heterogeneity among plots. Brand and Parker (1994) emphasize, however, that disturbance is but one of many "environmental inputs to continuous, interactive, dynamic processes, each of which partially determines recruitment and survivability." They point out that many propagules may become established without disturbance, so site availability should not be thought of as just a product of disturbance. Viewed from the perspective of Brand and Parker's (1994) generalized model, vegetation dynamics of this sagebrush steppe can be understood as the ongoing interactions between a spatially and temporally heterogeneous environment and a suite of species that differ in dispersal capacities and in their potential for establishing and/or persisting under varying environmental conditions.

Cover data for perennial grasses and shrubs indicate that, at least in certain years, competition may impact the abundance of some species. There were significant negative correlations between grass cover and shrub cover in years when the abundances of these groups were highest. The pattern of change in cover of these two groups suggests that grass cover is constrained on plots with greater shrub cover (Fig. 14). These data are consistent with the hypothesis that biotic interactions, such as competition or predation, can play important roles in determining the distribution and abundance of plant species at the site, but that their effect is controlled by the availability of water. Because the availability of water is highly variable in time, the responses of vegetation to changes in the type and intensity of disturbance probably take longer here than in many other systems that are limited by resources that are less variable in time. Furthermore, the large variation in precipitation on both year-to-year and longer-term time scales may be important in insuring the coexistence of shrubs and perennial grasses in this ecosystem. That variation contributes to the dynamics that precludes convergence on a stable species composition at the scale of an individual sample plot.

*Relationships between species diversity, cover and stability.* Tilman et al. (1996) reported positive correlations between vascular plant cover and species diversity in experimental plots and in native savanna in east central Minnesota. These results, together with earlier reports of a link between species diversity and resilience to drought (Tilman and El Haddi 1992, Tilman and Downing 1994) provide additional evidence for a link between plant species diversity and functional properties of ecosystems (McNaughton 1977). We found similar relationships in an ecosystem having different dominant species, a different dominant growth form, and lower overall vegetative cover than that studied by Tilman and colleagues. Cover was higher on plots having

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more species, and this was true for shrubs and perennial grasses separately and for the two groups combined.

An obvious interpretation of these relationships is that in plots having more species there was better use of limiting resources because of species-specific differences in resource acquisition patterns and therefore those plots produced higher total vegetative cover (Tilman et al. 1996). Tilman et al. offered evidence of more complete utilization of available soil nitrogen on plots having more plant species. It is not clear what differences in resource acquisition might have contributed to this pattern in this sagebrush steppe, but nitrogen is a limiting resource here as well (Toft et al. 1989), and Bilbrough and Caldwell (1997) found differential responses to pulses of nitrogen among sagebrush steppe species. They speculated that competition is likely intense for early-spring nitrogen pulses.

Unlike the grasslands of Minnesota, this shrub steppe vegetation is clearly water limited and plants extract virtually all of the available soil moisture each year (Anderson et al. 1987). Anderson et al. found that seasonal patterns of water use were similar among four dominant perennial species and attributed that similarity to the strongly seasonal availability of soil moisture. Thus, temporal partitioning of water use within the growing season does not appear to provide a basis for differential resource use among dominant species in the system that would account for the observed relationships between diversity and cover. An alternative explanation is that when more species are present it is more likely some species will be better able to take advantage of the prevailing environmental conditions in a given year (Huston 1997). This sort of temporal niche partitioning with respect to year-to-year variability in climate is thought to promote co-existence among species (Chesson and Huntly 1989, 1993, 1997), and it may in turn contribute to maintenance of higher mean levels of productivity and to reduced relative variability in productivity among years.

We found, as did Tilman (1996), that the relative change in cover from year to year was negatively correlated with species richness; however, the magnitude of variation in absolute cover was positively correlated with species richness (Fig. 13). This outcome is consistent with the idea that higher richness increases the probability of a species being present that can vigorously respond to favorable conditions such as abundant rainfall.

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It is also possible that the observed relationships between species richness and cover reflect a productivity gradient among the plots. Along a gradient from very low to high productivity, diversity typically is highest at intermediate levels (Grime 1973). In a sagebrush steppe, where productivity may be severely constrained by water availability and edaphic factors including shallow soils, we would expect plots to vary in their capacity to produce biomass. A higher capacity for biomass production on some plots may allow more species to survive (Huston 1997).

The data from the permanent plots do not provide a basis for choosing among these alternatives. Nevertheless, the correlations between richness, cover, and variation in cover are highly significant and show that, regardless of the cause, plots having greater species richness tend to vary less in cover, and presumably in productivity, in relation to their mean level. Plots having greater species richness also tend to maintain higher levels of cover.

*The core versus the peripheral plots.* Similar changes have occurred on the core and peripheral plots. These include a large increase in shrub cover during the first 2 to 3 decades, large increases in the abundance of perennial grasses since 1950, increases in mean richness per plot, and an increase in heterogeneity among plots. The overall structure of the vegetation on the two groups of plots was also quite similar at the most recent sampling (1995, Tables 1, 3). Total vascular plant cover was almost identical on the core and peripheral plots and the contributions of shrubs and perennial grasses to total cover were similar. Relative cover of perennial forbs was also similar (7.7% vs 10.3% on the core and peripheral plots, respectively). The major difference between the two sets of plots was in cover of annuals and biennials. This group contributed 25% of the vascular plant cover on the core plots, but only 13% on the peripheral plots. The numbers of annuals and biennials were similar on the core and peripheral plots, but their contributions differed substantially. Cover of native and introduced annuals on the core plots was essentially equal, whereas on the peripheral plots native annuals and biennials produced twice the cover of introduced ones.

These are not the results that one might have expected in a comparison of a grazed vs an ungrazed area, but, as we have emphasized in Methods, it would be inappropriate to attribute any of the results to differences in livestock grazing because the sample is not representative of the grazed area and because of various confounding variables. The higher abundance of exotics on

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the core plots may simply reflect higher availability of suitable habitat. Aside from those differences, it seems reasonable to conclude that the same mechanisms have been responsible for the roughly parallel changes since 1950 on the core and peripheral plots.

*Invasion of Bromus tectorum.* Data from the long-term vegetation plots indicate a very rapid expansion of the distribution of *B. tectorum* at the INEEL in the decade between 1965 and 1975, and the number of plots upon which it was recorded has generally increased in more recent samples (Table 2). This occurred in the absence of any major disturbance to the area sampled by the core plots. Clearly, *B. tectorum* can invade native vegetation without facilitation by disturbances such as livestock grazing or fire. Does this imply that conversion of the vegetation at the INEEL to *B. tectorum*-dominated annual communities, such as has occurred elsewhere on the Snake River Plain (e.g., Whisenant 1990) is inevitable? We doubt this will be the case, so long as healthy populations of native species are maintained. The distribution of *B. tectorum* at the INEEL is somewhat limited by edaphic factors; it occurs rarely and does not do well on sites having fine textured clayey soils (Rasmuson 1996), such as occur on the playas and lakebed sediments of Pleistocene Lake Terreton. Although *B. tectorum* has spread to most areas having coarser textured soils, it has displaced the native vegetation on those areas infrequently. On Plot 86, *B. tectorum* was rare in 1985, but accounted for over half of the vascular plant cover in 1990 and 1995. Such examples are uncommon, however, and the bulk of the evidence available suggests that because native plant populations are generally thriving at the INEEL, *B. tectorum* does not pose the threat that it does elsewhere. The exception may be on areas subject to heavy grazing where native plant populations have been severely impacted. *B. tectorum* has become a dominant species on several thousand hectares on the northeast side of the INEEL that have been heavily grazed by sheep in recent years (R. Blew, personal communication). Additional research and monitoring should be undertaken in an effort to more fully understand the potential for conversion of native steppe to fire-prone annual communities.

*Management implications.* Designation of the INEEL as a National Environmental Research Park in 1975 emphasized its importance as a field laboratory for ecological research. Subsequent research has shown that the INEEL is a unique reservoir of the genetic diversity of sagebrush steppe, supporting some 400 species of vascular plants (Anderson et al. 1996) and a rich complement of native animals. Compared with areas that have a long history of livestock grazing, the INEEL supports a rich diversity of native forbs. Eighty-five percent of the species are natives,

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and three-fourths of those are forbs. Data from the permanent vegetation plots are among the most comprehensive long-term data sets for any terrestrial ecosystem. Every effort should be made to maintain the integrity of the permanent plots and to ensure that they are sampled periodically. Anthropogenic disturbances at the INEEL should be minimized, especially on the "core area" – that area currently closed to livestock grazing. The current grazing boundary should be maintained and enforced. A monitoring program should be implemented to ensure that livestock grazing on the peripheral area does not degrade the vegetation. As noted above, some areas have been severely impacted within the last two decades.

The sheer size of the core area makes it unique among protected areas of sagebrush steppe. This is an area large enough to study landscape-level processes and to accommodate natural population fluctuations and disturbance regimes. The core area should be managed as a natural preserve, insofar as possible. This would include allowing wildfires to run their course so long as they did not threaten facilities. We recommend that existing roads and natural fire breaks (e.g., lava outcrops, the Big Lost River) be used to control fires whenever possible and that new fire lines be cut only when necessary to protect facilities. Data from areas burned in large fires at the INEEL in 1994 and 1995 indicate that on most areas native species will recover and dominate the vegetation on burned areas, so there is no need to artificially seed areas that have burned (S. Patrick and J. Anderson, unpublished data) so long as healthy populations of native species were present before the fire. Areas subjected to human disturbances that destroy vegetation should be quickly revegetated with native species. Introduction of non-native species should be avoided, and an aggressive weed control program to limit the spread of noxious weeds such as musk thistle (*Carduus nutans*), Dyer's woad (*Isatis tinctoria*), spotted knapweed (*Centaurea biebersteinii*), and yellow star thistle (*Centaurea solstitialis*) should be implemented. Because of their persistence and ability to invade undisturbed native vegetation (Marlette and Anderson 1986), further introductions of crested wheatgrasses (*Agropyron cristatum* and *A. desertorum*) should be restricted to severely disturbed sites such as waste management areas or landfills.

We do not have sufficient data to recommend changes to management on the areas open to livestock grazing. However, the observed lags in responses of species or life forms to precipitation suggest that stocking rates should be based on more than the current year's precipitation. It seems clear from the data that once this system becomes degraded (e.g., depauperate of species, low perennial grass cover), whether from prolonged drought, excessive

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grazing, or both, it will likely take decades to recover. Modest stocking rates with periodic rest may be necessary to allow recruitment and long-term maintenance of typical levels of diversity in the system. Positive relationships between diversity and cover indicate that maintenance of high levels of diversity would also help maintain high productivity. Thus, a conservative grazing strategy is warranted.

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